

# Characteristics of submarine cave bivalves in the northwestern Pacific

Itaru Hayami<sup>1</sup> and Tomoki Kase<sup>2</sup>

<sup>1</sup> Kanagawa University, Tsuchiya, Hiratsuka, 259-12, Japan

<sup>2</sup> National Science Museum, Shinjuku-ku, Tokyo 160, Japan

**Abstract:** This paper discusses the diversity, common features, and geographic distribution of submarine cave bivalves collected with SCUBA from a number of islands around the Philippine Sea (Okinawa, Miyako, Yonaguni, Daito, Bonin, Bohol and Cebu of the Philippines, Palau, and Guam). Common significant characteristics of cave bivalves are: (1) unique taxonomic assemblage, (2) reduced adult size, (3) many deep-water genera, (4) occurrence of several "cavity-dwelling" shallow-water genera on the exposed wall and sediment surface, (5) frequent paedomorphosis by progenesis, (6) relative abundance of non-planktotrophic species, (7) low fecundity and dominance of brooding, and (8) archaic life mode reminiscent of a fauna before the "Mesozoic marine revolution" (rarity of sedentary species and deep burrowers). These features must be related to one another and are generally regarded as due to a common adaptive strategy toward the oligotrophic condition and low predation pressure of cave habitats. It is still mysterious how cave bivalves, even brooding species, have become so extensively distributed in the western Pacific region. Although there is no positive evidence, rafting is a possible mechanism of transoceanic dispersal for minute epibyssate bivalves.

For several years now, we have been studying the cryptic biota of submarine caves with the assistance of several taxonomists and skilled divers. The cave organisms, although their biomass per unit area is very small, include various invertebrate groups such as benthic foraminiferans, sponges, sclerosponges, solitary corals, gorgonians, polychaetes, bryozoans, brachiopods, sipuncules, ostracods, isopods, and echinoids in addition to gastropods and bivalves. Among others, the taxonomic diversity and evolutionary significance of cave mollusks (especially bivalves) were partly elucidated on the basis of numerous samples collected by SCUBA divers from the Ryukyu Islands (Okinawa and Miyako) (Kase and Hayami, 1992; Hayami and Kase, 1992, 1993). More than 45 species have been systematically described by us.

Subsequently, we expanded the area of our study and explored many caves on other islands around the Philippine Sea, namely Yonaguni Island of Ryukyu (one cave), Minami-daito Island (one cave), Chichijima Islands of Bonin (six caves and interior of some sunken ships), Panglao Island of Bohol (three caves), Mactan Island of Cebu (one cave), "Rock Islands" of Palau (six caves), and Guam (two caves) (Fig. 1). Some samples from Guam and Saipan in the synoptic collection of the Marine Laboratory, University of Guam, were also examined. Although living specimens were not necessarily abundant in these newly explored caves, it became clear that many cave bivalves are

widely distributed among these distant islands. Up to now, about 60 bivalves have been recognized as cavernicolous. The present paper discusses the common characteristics of cave bivalves as well as their geographic distribution.

## SUBMARINE CAVES AROUND THE PHILIPPINE SEA

More than 30 surveyed caves in this region vary in size and topography, but mostly are sublittoral meandering limestone grottoes. Their entrances (Fig. 2) lie between sea level and 40 m, and their lengths range from several meters to more than 70 m. In several relatively flat islets of the Ryukyu Islands numerous caves are open to fore-reef slopes, the mother rock of which is the Pleistocene Ryukyu Limestone. They were undoubtedly formed by underground water during some lower sea-level stage and finally drowned in the post-glacial sea-level rise. If the Pleistocene-Holocene sea-level change in this region is considered, all the marine organisms in these caves must have originated sometime after 10,000 years B.P.

Owing to the low physical energy of the sea water, sediments on the floor of deep caves are generally very fine except for organic remains, and almost free of coarse terrigenous material. Because these caves are already hydrologically inactive, the temperature and salinity of the cave

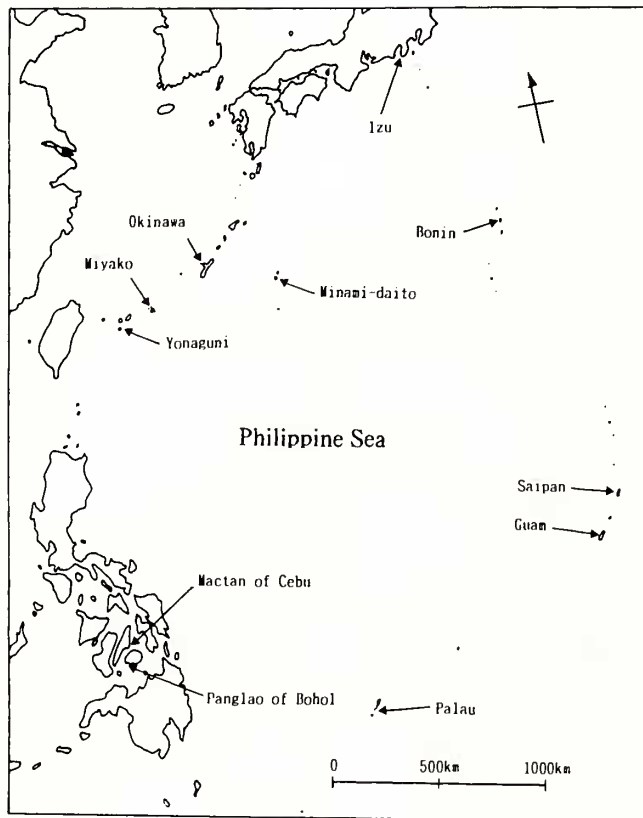


Fig. 1. Map showing the localities of marine cave samples.

waters are almost equal to those of the open sea throughout a year. Tubular sediment cores taken successfully by a cooperative diver at the innermost part of some caves indicate that the environment seems to have been maintained under tranquil but never oxygen-depleted conditions. Many surveyed limestone caves in other islands seem to be basically similar to those of the Ryukyu Islands in physico-chemical conditions.

In Okinawa, Yonaguni, Bonin, Bohol, and Palau, the twilight wall and ceiling near the cave entrances are often inhabited by sclerosponge fauna, which consists of sclerospoenges, articulate brachiopods, bryozoans, and ahermatypic hexacorals. This cryptic fauna corresponds to "the brachiopod-coralline sponge community," which was recognized by Jackson *et al.* (1971) mainly in the Caribbean Sea. In the present region it is commonly accompanied by *Pycnodonte taniguchii* (a large archaic oyster) (Hayami and Kase, 1992). *Glossocardia obesa* is another exceptionally large bivalve in the cave fauna. In Ryukyu and Palau this clam inhabits poorly lit soft bottom in a number of caves.

Toward the totally dark inner part the biomass becomes much smaller, and the wall and ceiling are rarely covered with encrusting organisms, although *Neritopsis radula* (Linné, 1758) (a well-known "living-fossil" gastro-

pod), *Dimyella* spp. (small characteristic sedentary bivalves), thecidellinid brachiopods, and some soft sponges are often found. Moreover, the sediment surface is inhabited by many minute bivalves and other invertebrates such as benthic foraminiferans, gastropods (mostly archaeogastropods), sipuncules (commonly dwelling in gastropod shells), ostracods, and isopods.

It is a fundamental question whether or not these minute bivalves are really indigenous to such sheltered environments. Because the distribution of such minute bivalves has not been sufficiently studied in this region, it is now difficult for us to give an obvious answer to this question. More than 60 bivalves (Table 1), however, are regarded as cavernicolous (if not strictly indigenous to caves), because they are actually represented by numerous living specimens (or fresh empty shells). The possibility of concentration of immature individuals must be also examined. In many cases, however, asymptotic size distribution indicating adult size and other lines of evidence (*e.g.* parental care of juveniles) seem to deny the possibility of invalid dispersal.

## CHARACTERISTIC FEATURES OF CAVE BIVALVES

### UNIQUE TAXONOMIC COMPOSITION

The Arcoidea, Limopsoidea, Mytiloidea, Pectinoidea, Limoidea, and Carditoidea are the dominant superfamilies in these caves, not only in species diversity but also in number of individuals. These superfamilies are also common in the exposed environment of the same region, but the familial and generic composition of the cave assemblages are unique. In some caves a species of *Huxleyia* (Nucinelloidea) is also dominant.

The cave Arcoidea consist of several species of *Bentharca* (though atypical) and *Bathyarca*, and the species of the Limopsoidea mostly belong to *Philobrya*, *Cosa*, and *Cratis* of the Philobryidae. All of the cave Pectinoidea belong to *Parvamussium*, *Cyclopecten*, and *Chlamydella* of

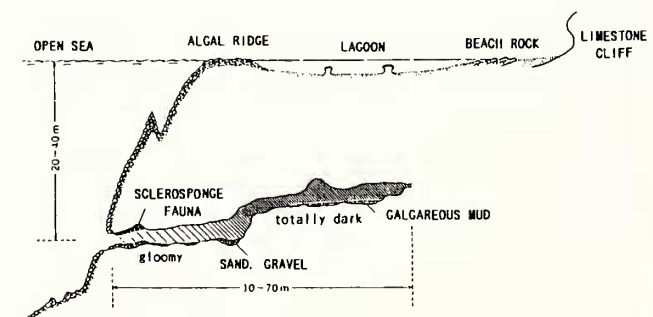


Fig. 2. Diagrammatic section of a submarine cave in the Ryukyu Islands.

**Table 1.** Distribution and characteristics of cave bivalves in the northwestern Pacific. Bh, Bohol; Bn, Bonin; Dm, Minami-daito; DWG, deep-water genus; Gm, Guam; Hw, Hawaii (not cave); Js, South Japan (not cave); My, Miyako; NP (BR), non-planktotrophic (brooding); Ok, Okinawa; Pl, Palau; PRG, paedomorphic (by progenesis); STD, stunted; Yn, Yonaguni; ●, living; ○, empty shells.

| Species name (Hayami and Kase, 1993)<br>(*undescribed species) | Distribution |    |    |    |    |    |    |    |    |    | Characteristics |     |     |        |
|--|--------------|----|----|----|----|----|----|----|----|----|-----------------|-----|-----|--------|
|  | Js           | Ok | My | Yn | Ds | Bn | Bh | Pl | Gm | Hw | STD             | DWG | PRG | NP(BR) |
| <i>Solemya (Petrasma)</i> sp.                                  |              |    | ●  |    |    |    |    |    |    |    |                 |     |     |        |
| <i>Huxleyia cavernicola</i> Hayami and Kase, 1993              |              | ○  | ●  |    |    | ●  | ○  | ○  |    |    | +               | +   | +   | +      |
| <i>Pronucula insignis</i> Hayami and Kase, 1993                |              | ○  | ●  |    |    |    |    |    |    |    | +               | +   | +   | +(+?)  |
| <i>P.?</i> sp. *   | ○            |    |    |    |    | ●  |    |    |    |    |                 |     |     |        |
| <i>Acar</i> aff. <i>plicata</i> (Dillwyn, 1817)                |              | ○  | ○  |    | ○  | ○  | ○  | ○  |    |    | +               |     |     |        |
| <i>Bentharca tenuis</i> Hayami and Kase, 1993                  |              | ○  | ●  | ○  |    |    | ○  | ?  | ?  |    | +               | +   | +   | +      |
| <i>B. decorata</i> Hayami and Kase, 1993                       |              | ○  | ○  |    |    |    |    |    |    |    | +               | +   | +   | +(+?)  |
| <i>B. irregularis</i> Hayami and Kase, 1993                    |              | ○  | ○  |    |    |    | ○  |    |    |    | +               | +   | +   |        |
| <i>B. excavata</i> Hayami and Kase, 1993                       |              | ●  | ●  |    |    |    |    | ○  |    |    | +               | +   | +   | +      |
| <i>B. sp. A</i> *  | ○            |    |    |    |    | ●  |    | ○  | ○  |    | +               | +   | +   |        |
| <i>B. sp. B</i> *  |              |    |    |    |    |    |    |    |    | ○  | +               | +   | +   |        |
| <i>Batharca</i> sp.  |              |    | ○  |    |    |    |    |    |    |    | +               | +   | +   | +      |
| <i>Philobrya</i> sp. *   |              |    |    |    | ●  |    |    |    |    |    |                 |     | +   | +(+?)  |
| <i>Cosa waikikia</i> (Dall, Bartsch and Rehder, 1938)          | ○            | ●  | ●  | ○  |    | ●  |    | ○  |    | ○  |                 |     | +   | +(+)   |
| <i>C. kinjoi</i> Hayami and Kase, 1993                         |              | ●  | ●  | ○  |    |    | ○  | ○  |    |    |                 |     | +   | +(+?)  |
| <i>C. uchimae</i> Hayami and Kase, 1993                        |              | ○  |    |    |    |    |    |    |    |    |                 |     | +   | +(+?)  |
| <i>C. sp.</i>  |              |    | ○  |    |    |    | ○  |    |    |    |                 |     | +   | +(+?)  |
| <i>Cratis kanekoi</i> Hayami and Kase, 1993                    | ○            |    | ○  |    |    |    |    |    |    |    |                 | +   | +   | +(+?)  |
| <i>Cratis</i> cf. <i>kanekoi</i> *                             |              |    |    |    |    |    |    |    | ○  |    |                 | +   | +   | +(+?)  |
| <i>C. ohashii</i> Hayami and Kase, 1993                        | ○            | ○  | ○  |    |    |    |    |    |    |    |                 | +   | +   | +(+?)  |
| <i>Limopsoidea?</i> gen. and sp. indet.                        |              | ○  | ○  | ○  |    |    | ○  | ○  | ○  |    |                 |     |     | +      |
| <i>Brachidontes</i> sp.  |              | ○  | ○  |    | ○  |    |    |    |    |    |                 |     |     |        |
| <i>Septifer</i> sp.  |              |    | ●  | ○  |    |    | ○  | ○  |    |    |                 |     |     |        |
| <i>Crenella</i> sp. A  |              | ○  | ●  |    |    |    | ○  |    |    |    | +               |     | +   | +      |
| <i>C. sp. B</i> *  |              |    |    |    | ○  | ●  |    |    |    |    | +               |     |     |        |
| <i>Dacrydium zebra</i> Hayami and Kase, 1993                   |              | ●  | ●  | ○  | ●  | ●  | ○  | ○  |    |    |                 | +   | +   | +(+)   |
| <i>Urumella concava</i> Hayami and Kase, 1993                  |              |    | ●  | ○  |    |    | ○  |    |    |    |                 |     | +   | +      |
| <i>Malleus (Malvufundus)</i> sp.                               |              | ●  | ●  |    |    | ●  |    |    |    |    | +               |     |     |        |
| <i>Parvamussium crypticum</i> Hayami and Kase, 1993            |              | ●  |    |    | ○  |    |    |    |    |    | +               | +   |     | +      |
| <i>P. cf. crypticum</i> *                                      |              |    |    |    |    |    |    | ●  |    |    | +               | +   |     | +      |
| <i>P. decoratum</i> Hayami and Kase, 1993                      | ●            |    | ●  | ○  |    |    |    |    |    |    | +               | +   |     | +      |
| <i>Cyclopecten ryukyuensis</i> Hayami and Kase, 1993           |              | ○  | ●  | ○  |    |    | ○  | ○  |    |    | +               | +   |     | +      |
| <i>Chlamydeila incubata</i> Hayami and Kase, 1993              | ○            | ○  | ●  |    |    | ●  | ○  | ○  | ○  |    | +               | +   |     | +(+)   |
| <i>C. tenuissima</i> Hayami and Kase, 1993                     | ○            |    | ●  |    | ●  | ●  |    |    |    |    | +               | +   |     | +(+)   |
| <i>Dimyella</i> sp. A *  |              | ●  |    |    |    |    | ○  |    |    |    |                 |     |     |        |
| <i>D. sp. B</i> *  |              |    |    |    |    |    |    | ○  | ○  |    |                 |     |     |        |
| <i>Pycnodonte taniguchii</i> Hayami and Kase, 1992             |              | ●  | ●  | ●  | ○  | ●  | ●  | ●  |    |    | +               |     | +   | +      |
| <i>Lima</i> sp.  |              | ○  | ●  |    |    |    | ○  | ○  |    |    | +               |     | +   | +      |
| <i>Divarilima elegans</i> Hayami and Kase, 1993                |              | ○  |    |    |    |    |    |    |    |    | +               | +   |     | +      |
| <i>Ctenoides minimus</i> Hayami and Kase, 1993                 |              | ○  | ●  |    | ○  |    |    | ○  |    |    | +               |     | +   | +      |
| <i>Isolimea limopsis</i> (Nomura and Zinbo, 1934)              | ○            |    | ○  |    |    |    |    |    |    |    |                 |     |     | +      |
| <i>Limatula kinjoi</i> Hayami and Kase, 1993                   |              | ○  | ●  |    |    |    |    |    |    |    | +               |     |     | +(+?)  |
| <i>Limaria</i> sp.   |              | ○  | ●  |    |    |    |    | ○  |    |    |                 |     |     |        |
| <i>Epicodakia pygmaea</i> Hayami and Kase, 1993                |              | ○  | ●  |    | ○  |    |    | ○  |    |    | +               |     |     |        |
| <i>Cardita uruma</i> Hayami and Kase, 1993                     |              | ●  | ●  |    |    |    |    |    |    |    | +               |     |     |        |
| <i>C. sp. A</i>  |              | ○  |    |    |    |    |    |    |    |    | +               |     |     |        |
| <i>C. sp. B</i> *  |              |    |    |    | ○  |    |    |    |    |    |                 |     |     |        |
| <i>Carditella iejimensis</i> Hayami and Kase, 1993             |              | ●  |    |    |    |    |    |    |    |    | +               | +   |     | +      |
| <i>C. shimoiensis</i> Hayami and Kase, 1993                    |              |    | ●  |    |    |    |    | ○  |    |    | +               | +   |     | +      |
| <i>C. sp. *</i>  |              |    |    |    |    |    |    |    | ○  |    |                 |     |     |        |
| <i>Condylocardia</i> sp. *                                     |              |    |    |    |    | ●  | ○  |    |    |    |                 |     |     | +(+?)  |
| <i>Salaputium unicum</i> Hayami and Kase, 1993                 |              | ○  | ●  |    |    |    |    |    |    |    | +               | +   |     | +      |
| <i>S.?</i> sp. *   |              |    |    |    |    |    |    | ○  |    |    |                 |     |     |        |
| <i>Rocheffortina sandwichensis</i> (Smith, 1885)               | ○            | ○  | ●  | ○  | ○  | ●  | ○  | ○  |    | ○  |                 |     | +   |        |
| <i>Kelliella japonica</i> Hayami and Kase, 1993                |              | ○  | ○  |    |    |    |    |    |    |    |                 | +   |     |        |
| <i>Coralliophaga hyalina</i> Hayami and Kase, 1993             |              | ○  | ●  |    | ○  |    | ○  | ○  | ○  |    | +               |     | +   |        |
| <i>Glossocardia obesa</i> (Reeve, 1843)                        |              | ●  | ●  |    | ○  |    |    | ●  | ○  |    |                 |     |     |        |
| <i>Exotica</i> sp. *   |              |    |    |    |    | ●  |    |    |    |    |                 |     |     |        |
| <i>Irus (Irus)</i> sp.   |              |    | ●  |    |    |    | ○  |    |    |    |                 |     |     |        |
| <i>I. (Notirus)</i> sp.  |              | ○  | ●  |    |    |    |    |    |    |    |                 |     |     |        |
| <i>Hiatella</i> aff. <i>orientalis</i> (Yokoyama, 1920)        | ○            |    | ○  |    | ○  | ○  | ○  |    |    |    | +               |     |     |        |
| <i>Halonympha asiatica</i> Hayami and Kase, 1993               |              | ○  |    |    |    |    |    |    |    |    | +               | +   |     | +      |
| <i>Austroneaera</i> sp. *                                      |              |    |    | ○  |    |    |    | ○  |    |    |                 | +   |     |        |



the Propeamussiidae (rather than Pectinidae). The occurrence of *Huxleyia*, *Pronucula*, *Dacrydium*, *Divarilima*, *Carditella*, *Kelliella*, and *Halonympha* is remarkable, because these genera have been scarcely represented in the upper sublittoral faunas of this region. The discovery of two undescribed species of *Dimyella* is also noteworthy, because this genus was originally proposed for a cave species in the Caribbean region (Moore, 1970). In contrast, the Nuculanoidea, Pinnoidea, Pterioidea, Anomioidea, Ostreoidae, Chamoidea, Cardioidea, Mactroidea, Tellinoidea, Solenoidea, Veneroidea, Myoidea, and Pholadoidea are very rare or entirely absent in these cave communities.

### REDUCED ADULT SIZE

Cave bivalves are generally very small. Most species are less than 6 mm in adult size. This may be the result of two different processes. One is the invasion of cave habitats by species belonging to clades characterized by small body size; for example, cave bivalves belonging to the Philobryidae, Condyllocardiidae, and Kelliellidae are not much smaller than closely related non-cavernicolous species in the same families. The other is true stunting, which may have occurred as a result of adaptation to such a sheltered environment. Cave species of *Huxleyia*, *Bentharca*, *Malleus* (*Malvufundus*), *Parvamussium*, *Cyclopecten*, *Chlamydella*, *Divarilima*, *Ctenoides*, *Limatula*, *Carditella*, *Coralliophaga*, and *Halonympha* are much smaller than all related species belonging to the same genus. In some cases (especially shallow-water genera) it is difficult to determine whether the size reduction reflects a species-level difference or is only ecophenotypic.

*Pycnodonte taniguchii* and *Glossocardia obesa* are exceptionally large species among the cave bivalves. They are, however, characterized by unusually reduced soft parts in comparison with the shell size.

### ABUNDANCE OF DEEP-WATER ELEMENTS

One of the striking characteristics of cave bivalve communities is the dominance of deep-water genera. *Bentharca*, *Batharca*, *Dacrydium*, *Kelliella*, and *Halonympha* are important abyssal genera (Knudsen, 1970; and others), and their abundant occurrence in upper sublittoral caves is remarkable. Curiously enough, the cave species of *Dacrydium*, *Kelliella*, and *Halonympha* are, even though specifically distinct, morphologically very similar to northern Atlantic abyssal species (Hayami and Kase, 1993).

*Huxleyia*, *Pronucula*, *Cratis*, *Parvamussium*, *Cyclopecten*, *Chlamydella*, *Divarilima*, *Carditella*, and *Austroneaera* are also regarded as deep-water elements, because most species of these genera occur at lower sublittoral and/or bathyal depths. The discovery of many deep-

water genera in sublittoral caves seems to indicate that hydrostatic pressure and water temperature are not necessarily decisive factors controlling the bathymetric distribution of bivalve genera. The similarity in generic composition between caves and deep waters may be attributed to other environmental factors in common, such as low light levels, oligotrophic conditions, and low predation pressures.

### EXPOSED LIFE OF SOME "CAVITY-DWELLING" BIVALVES

Cave bivalve communities also contain a number of species belonging to shallow-water genera, but their microhabitat and mode of life are not necessarily the same as those in non-cavernicolous environments. For example, *Barbatia decussata* (Sowerby, 1833), is one of the most ubiquitous bivalves on the rocky shores of the Palau Islands. This species predominantly dwells in narrow rock and coral cavities, whereas in the "Chandelier Cave" of the same islands, numerous individuals were found alive on the exposed wall surface. In many caves of the Ryukyu Islands, *Coralliophaga hyalina*, and *Irus* spp. are found alive on the sediment surface, notwithstanding that ordinary species of these genera are cavity-dwellers. Low predation pressure in the caves could be the most plausible explanation for the occupation of more exposed microhabitats by these species.

### DOMINANCE OF PAEDOMORPHIC EVOLUTION

Cave bivalves often exhibit paedomorphic evolution. In many species of the Pteriomorphia, denticles of the provinculum are persistent through all growth stages. In the Arcidae the number of adult teeth increases with growth, but is consistently small in cave species. In many cave species of *Bentharca*, the duplivincular ligament is still undeveloped and the primary, alivincular ligament remains active throughout growth. Paedomorphosis is also apparent in *Huxleyia cavernicola* and in all the cave species of the Philobryidae, Mytilidae, and Limidae. Some authors have regarded many genera of the Philobryidae, *Dacrydium*, and *Kelliella* as neotenous, but, considering the remarkable reduction of adult size, the prevailing heterochrony in these cave bivalves should be regarded as progenesis (instead of neoteny) as defined by Gould (1977) and McKinney and McNamara (1991).

### ABUNDANCE OF NON-PLANKTOTROPHIC SPECIES

The prodissoconch of cave bivalves is generally well-preserved without abrasion and erosion in both living specimens and empty shells, probably because of the low-energy conditions and oversaturation of calcium carbonate in the sea water prevailing in cave habitats. The size and shape of prodissoconch I and the presence or absence of

prodissoconch II seem to indicate egg size and larval developmental mode (planktotrophic, lecithotrophic, or directly developed) to a certain extent (Ockelmann, 1965; Jablonski and Lutz, 1980, 1983).

Applying Ockelmann's (1965) criteria for the relation between prodissoconch I size and developmental type, the proportion of non-planktotrophic species among cave bivalves from the Ryukyu Islands is as high as 70% (Fig. 3). Though no reliable statistical study has been carried out for non-cryptic bivalves in this region, this value seems to be unusually high for bivalves in low-latitudinal sublittoral seas and rather comparable with the ratios of high-latitudinal (Ockelmann, 1965) and deep-water (Knudsen, 1970) faunas.

### LOW FECUNDITY AND DOMINANCE OF BROODING SPECIES

Incubation of several juveniles has been well-recognized in *Cosa waikikia*, *Dacrydium zebra*, *Chlamydeella incubata*, and *C. tenuissima* (see Hayami and Kase, 1993). The presence of a large, hat-shaped prodissoconch I seems to indicate that *Bentharca decorata*, most species of the Philobryidae, *Limatula kinjoi*, and *Condylocardia* sp. are also brooding species. These facts also lead us to suspect that parental care of larvae may occur in more taxonomic groups (e.g. Arcidae, Propeamussiidae, and Limidae) than previously realized, and that the size and shape of prodisso-

conch I (and also developmental strategy) are quite changeable even within one genus.

In addition to the dominance of brooding species, low fecundity of many cave bivalves is generally suggested by their minute adult size and large prodissoconch I. The diameter of prodissoconch I, which reflects the egg size, often exceeds 1/10 of adult size. Although little is known about their growth rate and longevity, K-strategy seems to prevail in cave bivalves. Under such nutrition-poor conditions for suspension feeders, K-selection probably becomes more advantageous than wasteful r-selection.

From a theoretical viewpoint, K-selection has been considered to be commonly accompanied by neoteny (Gould, 1977; Pianka, 1983), but this is probably not the case with the present cave bivalves, as discussed by Jablonski and Lutz (1980) for high latitudinal and deep-water mollusks. The constantly low food levels (and thus potentially low carrying capacity) could be a decisive factor controlling the adaptive strategy of cave organisms. For cave bivalves stunting and progenesis might be the only adoptable strategy to survive under food-limited conditions. Low fecundity and brooding must be also effective under such conditions. The unusually reduced soft parts of *Pycnodonte taniguchii* and *Glossocardia obesa* could also be related to the same trophic factor.

### TAXONOMIC AND ECOLOGICAL PRIMITIVENESS

In addition to some "living fossil" species (e.g. *Pycnodonte taniguchii*), cave bivalves are generally archaic both in their taxonomic composition and mode of life. Although the fossil records of small-sized bivalve genera are still insufficiently known, most of the represented families are of Mesozoic or earlier origin.

The cave bivalves are mostly byssate or free-living epifaunal species, while sedentary species and deep burrowers are very rare. In the innermost part of caves *Dimyella* spp. (often accompanied by thecideidine brachiopods) are the only cementing bivalve, and all the free-living bivalves inhabit the sediment surface. Judging from core sediment samples taken in some caves of the Ryukyu Islands, the tiering of burrowing organisms is very narrow, scarcely exceeding 10 mm below the sediment surface. There are no boring gastropods (naticids and muricids), and other durophagous animals seems to be rare in these caves, although some nocturnal fish, crabs, and lobsters dwell there in the daytime.

The defenseless features of cave bivalves reminds us of the fauna before the "Mesozoic marine revolution" (Vermeij, 1977, 1987). Submarine caves are generally characterized by low predation pressure and offer suitable refuges to ecologically archaic organisms.

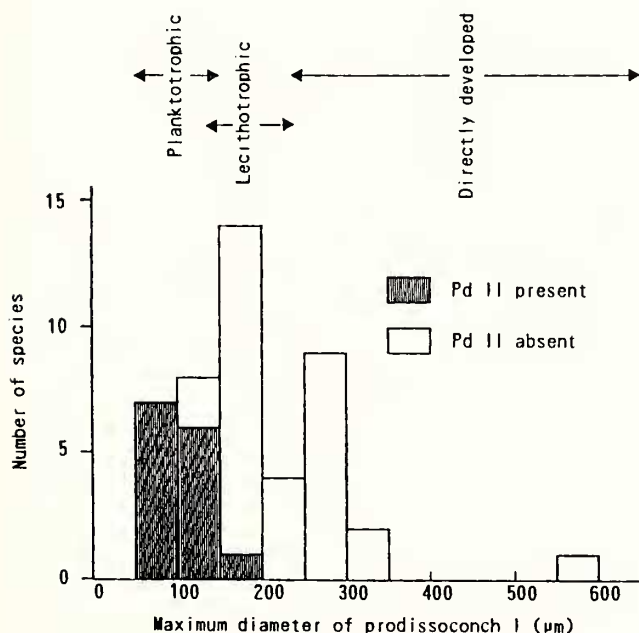


Fig. 3. Size distribution of prodissoconch (Pd) I in 45 cave bivalves from the Ryukyu Islands. Ockelmann's (1965) criteria for the types of larval development are shown above the histogram.



## GEOGRAPHIC DISTRIBUTION OF MARINE CAVE BIVALVES

Among about 60 cavernicolous bivalves, several species (e.g. *Cosa uchimae*, *Divarilima elegans*, *Carditella iejimensis*, and *Halonympha asiatica*) seem to be endemic to only one or two totally dark caves of Ie Islet of the Okinawa Islands. Numerous individuals of these species have been collected there, but none was found on other islands. *Philobrya* sp. is represented by numerous living specimens from a cave of Minami-daito Island, but philobryid faunas on other islands lack this species.

Most other bivalves, including many non-planktotrophic species, however, show wide geographic distribution in the northwestern Pacific. For example, *Dacrydium zebra*, *Chlamydelia incubata*, *C. tenuissima*, and *Condylocardia* sp. are certainly brooding species, but they are extensively distributed on many isolated islands around the Philippine Sea, which are far separated from one another by deep seas. *Rochefortina sandwichensis* and *Cosa waikikia*, which were originally described from Hawaii (Smith, 1885; Dall *et al.*, 1938), are known from a number of islands in this region (and also in Micronesia and the southern Pacific). Judging from the small size of prodissoconch I and the presence of prodissoconch II, the larvae of *Rochefortina sandwichensis* must be planktotrophic, but *Cosa waikikia*, at least in the Ryukyu Islands, is evidently a brooding species (Hayami and Kase, 1993: figs. 79-80).

All of the bivalves now living in these caves must have come from somewhere since the post-glacial sea-level rise, because during the Glacial Age the cave floors were above sea-level. In the Bonin Islands (Takinoura inlet of Anijima Island), some of these characteristic bivalves (including *Cosa waikikia* and *Chlamydelia incubata*) were found alive in the interior of several sunken ships (dating from World War II). These facts indicate that most cave bivalves can migrate rather easily in spite of their non-planktotrophic larvae and semi-closed habitats.

It is still an unsolved problem how cave bivalves without planktotrophic larval stages were able to extend their geographic distribution. Although the diversity and distribution of such small-sized bivalves are still insufficiently studied in this region, we hypothesize the following three possibilities for the wide geographic distribution of cave bivalves.

1. It is possible that these cave bivalves are extensively distributed and not necessarily indigenous to such a cryptic environment.

2. Developmental mode of bivalves could be more plastic than presently recognized. Ancestral planktotrophic populations could change their developmental strategy rapidly as an adaptation to caves.

3. Minute epibyssate species, even adult individuals,

could be able to migrate for a long distance by rafting. They could attach themselves to small floating objects or swimming animals.

At present, possibilities 1 and 2 cannot necessarily be denied, but, we suppose, they are rather unlikely for the following reasons. Empty shells of a few cavernicolous bivalves are occasionally found in beach sands of this region, but the species assemblages of minute bivalve shells in sediments on the beach and open sublittoral bottom are almost entirely different from those in the present cave samples. So far as we have examined, the size and shape of the prodissoconch (as well as adult morphology) in each cave species are considerably stable throughout the samples from distant islands. Parallel change of developmental mode at the adaptation to each cavernicolous habitat is, therefore, highly unlikely.

Ó Foighil (1989) extensively examined the developmental mode and geographic distribution of the cosmopolitan intertidal byssate bivalve genus *Lasaea* based on more than 150 museum samples. The results indicated that brooding species of *Lasaea* releasing crawl-away juveniles show wider geographic distribution than planktotrophic species of the same genus. It was pointed out that pelagic larvae are not necessary for long-distance dispersal in that genus, and that rafting has played a key role for the dispersal mechanism.

Rafting, as considered by several authors (Soot-Ryen, 1960; and others), could be an alternate dispersal method especially for minute byssate bivalves. Most of widely distributed cave bivalves without planktotrophic stages are small-sized and epibyssate like *Lasaea* species. In Miyako and some other islands we have actually observed that a large number of living individuals of *Cosa waikikia* and *Chlamydelia incubata* attach themselves to the exposed part of annelid tubes (Hayami and Kase, 1993: fig. 212) and soft sponges. Although there is no direct evidence, rafting could be the most important method for long-distance dispersal of these cave bivalves.

Iliffe and his coworkers surveyed marine troglobites (mainly crustaceans) in the subtropical northern Atlantic (Caribbean Sea, Bermuda, and Canary Islands), elucidating that several relict species inhabit the caves of these distant islands in common (Iliffe *et al.*, 1983, 1984). Ocean-floor spreading was once hypothesized as a cause for the amphiatlantic distribution of several relict crustaceans (Hart *et al.*, 1985). Furthermore, Iliffe (1990) discussed the possibility that the transoceanic dispersal of marine cave faunas could occur by way of deep-water caves and crevicular habitats. The hypothesis seems to be supported by the taxonomic resemblance between cave and deep-water faunas.

As noted before, a number of bathyal and abyssal genera are represented in the present cave bivalves. This is indeed one of the most remarkable characteristics, suggest-

ing that the cave bivalves are, at least in part, of deep-water origin. None of them, however, is strictly identical with any described deep-water species. Although we can by no means deny the possibility of gene flow between distant sublittoral caves via deep-sea bottom, there is not much evidence to support this dispersal method.

## CONCLUDING REMARKS

The bivalves collected from a number of marine sublittoral caves in several isolated islands around the Philippine Sea show striking and common characteristics such as reduced adult size, pedomorphosis by progenesis, dominance of non-planktotrophic larval development, and low fecundity. These features are probably related to one another and could have resulted from a common adaptive strategy to cavernicolous environments. Low food levels and low predation pressure are certainly the most important controlling factors. This conclusion seems to be also supported by the taxonomic resemblance of this fauna to deep-water bivalves and by the ecological archaism similar to the faunas before the "Mesozoic marine revolution."

Furthermore, the characteristics of cave bivalves seem to suggest the type of adaptive strategy that could be advantageous when extremely oligotrophic conditions prevail in the world. Although many problems (especially the process of migration and speciation) remain unsolved, we anticipate that the marine cave biota offers substantial data to test various theories in evolutionary biology.

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